

STUDIES IN PACIFIC COAST ENTOPROCTA.

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CONTENTS.

PLATE XVI.

	PAGE.
I. INTRODUCTION	323
II. MYOSOMA, GEN. NOV.....	324
<i>A. Structure</i>	324
1. THE STOLON.....	324
2. THE POLYPIDE	325
<i>a. The Calyx</i>	326
<i>b. The Stalk</i>	331
<i>c. The Neck</i>	331
<i>B. Regeneration</i>	332
<i>C. Discussion</i>	333
III. GONYPODARIA RAMOSA, SP. NOV.....	337
<i>A. Structure</i>	338
1. THE STOLON.....	338
2. THE STALK	338
3. THE CALYX.....	341
<i>B. Regeneration</i>	342
<i>C. Movement</i>	343
IV. SUMMARY.....	343
V. IDENTIFICATION OF KNOWN SPECIES.	344
BIBLIOGRAPHY	346
ABBREVIATIONS USED IN THE FIGURES	347
EXPLANATION OF PLATES	348

I. INTRODUCTION.

THE following studies were undertaken at the University of California under the direction of Professor W. E. Ritter, for whose cordial interest and unwearied kindness I wish to express my sincere gratitude.

The object of this paper is, first, to contribute to the knowledge of the Entoprocta by the description of two forms new to science, and secondly, to record the occurrence on the Pacific Coast of species already known. Of

the new forms, the one possesses features so markedly different from any known genus of the Pedicellinidæ as to warrant the formation of a new genus. The other is placed, at least provisionally, in the genus *Gonypodaria* Ehlers (1890).

Myosoma, gen. nov.

Diagnosis.—Zoarium with stolon composed partly of successive polypide-bearing segments and partly of alternate non-polypide-bearing segments; both stalk and calyx muscular, the muscle fibers continuous from one into the other; lophophore oblique.

Myosoma was obtained by Professor Ritter at Dillon's Beach near Tomales Bay, California. It has since been found at Fort Point and at San Pedro, California. As the name implies, its distinguishing generic characteristic is the possession of a muscular calyx, a feature not possessed by any other Entoproct known. Aside from the sphincter muscle, the Entoproct calyx is peculiarly destitute of muscular development. Ehlers (1890) describes certain muscle fibers in the calyx of *Ascopodaria macropus* which are connected with the nephridia, and others which he calls the lateral wall muscles. But in no case is there such a development as is found in this form.

Myosoma spinosa, sp. nov.

PLATE XVI, FIGS. 1-12.

Both stalk and calyx with surface differentiated into a spiny and a non-spiny region, the latter corresponding to the side of the polypide in which the musculature is more strongly developed.

A. Structure.

1. THE STOLON.—The colony of *Myosoma spinosa* forms a closely matted growth by the interweaving and fusion of its stolons. The stolon secretes a chitinous layer which is thicker on the under surface, and which serves both to attach itself to the substratum, and to unite adjacent stolons together laterally, thus forming a sort of band. From such a stolonical band, branches may extend laterally, both from

those stolons forming the outer border, and from the segments of any of the interior stolons. By this means a matted growth is produced which makes it impossible to tease out a colony without breaking it into small fragments. Figure 1 represents two stolons united for part of their length. It is not uncommon, however, to find four or more firmly united together. The stolon is segmented but not always to the extent that Ehlers considers characteristic of the Pedicellinidæ. Non-polypide-bearing segments (*non. pl. seg.*) occur, alternating with segments which bear polypides; but this is not the invariable rule. Polypides are frequently found upon successive segments, as is shown in the stolon extending to the right (fig. 1, *suc. seg.*). This drawing may seem to indicate that polypides are found upon successive segments only at the growing ends of stolons. This condition, however, is not confined to young stolons, but is found in older parts of the colony also. As an illustration of the variability of stolon segmentation presented by the species, I would say, that in twenty cases in which this point could be determined with certainty, twelve showed an intercalated non-polypide-bearing segment, while in eight cases, the polypides grew upon successive segments.

2. THE POLYPIDE.—Each polypide consists of an unbranched holosarcine stalk, and a calyx. There is considerable difference in the height of the various individuals which form a colony. Of ten polypides, all of which are adult so far as the functioning of the digestive organs are concerned, the smallest measures 0.64 mm. in height, and the tallest, 3.60 mm. The average height of the ten is 1.90 mm. The extreme mobility of the calyx, the obliquity of the tentacular region, and the spininess of both stalk and calyx are very conspicuous features of a colony.

In the retracted position, the stalk is usually much curved, the calyx being then brought face downwards, and the convex surface of both bristles with a formidable array of spines (figs. 1 and 2). Although I have not had an opportunity to examine living specimens, I cannot but

think that this peculiar curved position is one often assumed in life. On closer examination this conviction is strengthened, for the surface of both stalk and calyx is found to be differentiated into two regions, a spiny and a spineless one. The latter occupies a narrow strip extending from the base of the tentacles on the œsophageal side downward over the stalk to the stolon (figs. 1 and 2, *spl. reg.*). That this region possesses greater muscular power is apparent from a very casual examination of a glycerine mounted specimen. Figure 2 represents such a preparation. Here, in order to show the direction of the muscle fibers, the stalk is drawn in optical section. The spineless region (*spl. reg.*) and the longitudinal muscle fibers are seen to be on the same side.

Topographically, therefore, the surface of the polypide is divided into a ventral and a dorsal side. That part of stalk and calyx which possesses greater muscularity and which is free of spines is the ventral side; the spiny region is the dorsal. Throughout this description the terms ventral and dorsal, applied to both stem and calyx, will be used with this signification. Furthermore, although as we shall see, the connection between stalk and calyx is intimate, yet for purposes of description I will distinguish between them, and I will first describe the calyx.

(a). *The Calyx*.—The cuticle over the spiny region is thickened in places into ridges or ribs, upon which spines develop at regular intervals, although they are not lacking in other parts. One of these ridges is especially conspicuous, forming an almost circular rib at the base of the tentacles (fig. 1, *ten. r.*). It is thickened at the summit (fig. 1, *sum.*) of the tentacular disc and gradually grows more slender as it approaches the spineless region on the ventral side. Upon it six or eight spines are developed, forming a sort of coronet around the face, so to speak. From the summit of the calyx in the sagittal plane, a short, chitinous thickening of the cuticle extends forward upon the tentacular disc (fig. 1, *sag. r.*) This also bears one or more spines. Dorsally, in the sagittal plane, a double row of

spines extends to the base of the calyx, where another rib occurs which extends around it to the ventral side (fig. 1, *bas. r.*).

The Ventral Region.—Perhaps the most striking feature of the calyx is the extreme obliquity of the tentacular disc. This is so great that a point at the base of the tentacles on the dorsal side forms the summit of the calyx (figs. 1–2, *sum.*), and thus the whole tentacular region is on the ventral side. This, in the retracted condition, is a somewhat flattened oval disc which is bounded dorsally by the tentacular rib spoken of. In the center, an oval opening may be seen, around which the edge of the lophophore is gathered in strong folds by the sphincter muscle (figs. 1 and 2, *loph. f.*). Figure 3 is a para-sagittal section of the calyx and shows the sphincter muscle in cross-section (*sph. loph.*) and the fold of the lophophore projecting beyond it (*loph. f.*).

The cuticle on the ventral side is very thin, and is thrown into a number of transverse wrinkles or folds during contraction (fig. 3, *cu.*). Under the cuticle is a densely staining layer of ectodermal cells (fig. 3, *ec.*). Between the ectoderm and the œsophagus is found the somatic portion of the muscle which characterizes this form, and which, since it is to so large an extent continuous in both calyx and stalk, is designated as the *ventral muscle* (fig. 2, *v. mus.*).

The Musculature.—There are four systems of muscles in the calyx: viz., the somatic portion of the ventral muscle, the sphincter muscle, the tentacular muscles, and the muscles of the intestine.

The Ventral Muscle.—This muscle consists of a large number of bundles, each composed of a number of fibers. Scattered through it and at points of attachment are numerous large nuclei. Distally, it is attached to the body-wall of the calyx at the base of the tentacles. It extends in a longitudinal direction through calyx and stalk, and is attached proximally to the base of the stolon. The continuity of

some of the fibers is broken by the septum which separates calyx and stalk, but a *large number* of them pass through the septum *without interruption*.

The somatic portion of the ventral muscle and its direct continuation into the stalk are shown in fig. 3. This represents a para-sagittal section near the median plane. The space between the ventral body-wall (*v. w.*) and the œsophagus (*œs.*) is seen to be completely filled with longitudinal muscle fibers. At the focus which is here represented, many of these fibers are seen to pass over the septum into the stalk. At a deeper focus, the septum comes into view, bounded on each side by the large nuclei (*nu.*) which mark the attachment of those muscle fibers which are not continuous. At the base of the sphincter muscle (*sph. loph.*) the fibers are seen to unite with the ectoderm. In cross-sections of the calyx in this region, the intermingling of the longitudinal muscle fibers with those of the sphincter may be clearly seen. There can not, however, be said to be any direct union between the muscles of these two systems, although their union of action seems probable. Figure 4 is a frontal section close to the ventral wall of the stomach. Here the direct passage of a number of the muscle fibers (*v. m. f.*) from stalk to calyx is clear and undoubted. At each side the septum (*sep.*) is clearly seen through the continuous fibers, while in the middle there is a region where at the focus represented no septum is present. This section shows another interesting fact about the ventral muscle. When the fibers enter the calyx, some of them are seen to diverge right and left. These diverging fibers form branches of the somatic ventral muscle (*br. s. v. mus.*) which pass on each side of the œsophagus. The empty space in the center represents the position of the stomach at the base of the œsophagus. In a series of sagittal sections the branching is very evident, and furthermore, it is clear that part, at least, of these diverging fibers attach themselves to the floor of the atrium. In cross-section this is perhaps more evident. Figure 5 represents a cross-section of the stomach and base of the œsophagus. The somatic muscle fibers

(*so. v. m.*) which fill the space between the ventral wall (*v. w.*) and the œsophagus (*œs.*) are cut more or less obliquely. Close beside the œsophagus in the angle formed by its junction with the stomach (*st.*) are seen a few muscle fibers cut almost transversely. These are the branches of the somatic ventral muscle (*br. so. v. m.*). In sections above the plane represented by fig. 5, these transverse fibers become more distinctly grouped together and separated from the main body of the muscle (fig. 6, *br. so. v. m.*) They finally fuse with the floor of the atrium (fig. 7, *cls. at. fl.* and *br. so. v. m.*). In succeeding sections the atrial cavity appears and all signs of muscle bundles disappear. These branches may be called the atrial retractors, for by their contraction the floor of the atrium is drawn downward and the atrial cavity is enlarged.

All the muscle fibers which branch off from the ventral muscle do not, however, function as atrial retractors. Some of them seem to be in close connection with the genital duct, and perhaps with other organs. Figure 8 represents a section showing an apparent attachment of a muscle bundle (*m. g. d.*) on each side of the duct leading into the brood-sac. This section is just at the point where the duct (*cls. g. d.*) opens into the floor of the atrium (*at. fl.*) and taken in connection with indications found in other preparations, the inference seems to be a valid one that the ventral muscle is connected with the genital ducts in both males and females.

Sphincter Muscle.—When compared with other genera of Entoprocta, the lophophoral sphincter of *Myosoma* has an unusual development. According to Davenport (1893), the sphincter of *Urnatella* is composed of two or three fibers only. Ehlers gives seven or eight fibers for that of *Ascopodaria macropus*. An idea of the development which the sphincter attains in this form may be gained from fig. 3 (*sph. loph.*). Here the ends of the fibers appear, cut somewhat obliquely, in the deep fold of the lophophore (*loph. f.*). In frontal section, not represented in the drawings, this sphincter appears as a broad muscular band composed of twenty or thirty muscle fibers arranged in concentric circles.

Tentacular Muscles.—The number of tentacles varies between thirteen and fourteen. Each is provided with two muscles extending along the sides apparently to the tip. According to Davenport, tentacular muscles are unknown in any Entoproct except *Urnatella*. Comparing Davenport's drawing (Pl. IV, fig. 27) with fig. 9, it will be seen that *Urnatella* and *Myosoma* closely resemble each other in this respect. Figure 9 represents a cross-section near the base of three tentacles and the transverse ends of the tentacular muscle fibers are clearly shown (*tent. m.*). Figure 10 represents the same in longitudinal section, and the fibers (*tent. m.*) are seen extending through the length of the tentacles. The attachment of these fibers has not been definitely made out, but the indications are that they unite with the ectoderm at the base of the tentacular disc.

Intestinal Muscles.—In addition to the systems of muscles already described, there is an intestino-rectal sphincter. This consists of three or four well defined muscle bundles, showing in cross-section in the wall of the intestine. This is also reported for *Urnatella*. There is besides an anal sphincter, not differing apparently from that described for other Entoprocta.

The Organs.—The tentacles are ciliated on the inner surface. The atrial chamber is large and its floor is likewise ciliated. The alimentary tract does not differ materially from that described for other Entoprocts. It consists of œsophagus, stomach, intestine, and rectum, all heavily ciliated except the roof of the stomach, the region of the so-called "liver cells" (figs. 3 and 8, *cls. l.*). Figure 3 represents the alimentary tract, but the section is not in the median plane and consequently does not pass through the intestine and rectum.

No special study has been devoted to the nephridia, although the excretory ducts and pore have been observed. The nerve ganglion with its large nerve trunks is a conspicuous object, but no minute study of it has been made. Both males and females grow from the same stolon and are indifferently intermixed in the colony. The testes and the

ovaries contained ripe products, and the brood-sacs were filled with embryos in every stage of development.

(*b*). *The Stalk*.—Externally, the stalk shows the two regions, dorsal and ventral, already described for the calyx. The dorsal side is characterized by the presence of spines which, however, have no regular arrangement. The ventral side occupies about one-fourth of the circumference (figs. 11, 12, *v. s.*). The cuticle of this portion is thin and is thrown into many transverse wrinkles by the contraction of the muscles beneath (fig. 1, *spl. reg.*).

The Musculature.—The stalk is of the type holosarcine. The muscle forms a cylindrical sheath just beneath the ectoderm. The sheath, as a whole, is much thicker than in other Pedicellines, and its thickness is considerably greater on the ventral side than on the dorsal (figs. 11, 12, *v. m. stk.*). In the ventral region the fibers are longitudinal (fig. 2, *v. m.*). From a line in the middle of the dorsal region the fibers take an oblique direction on both sides toward the ventral side (fig. 2, *o. m. f.*).

In the lower part of the stalk and in the stolon just below the stalk, large granular cells, with very large nuclei, attract the attention, even in an unstained specimen. Frequently there are several processes to each cell. They are often found part way up the stem united together by these processes, resembling a string of beads. These are probably the myoblasts, from which the muscle fibers originate. The muscle fibers which are not continuous with those of the calyx are attached at their distal end to the septum between calyx and stalk. Proximally, both longitudinal and oblique fibers pass into the stolon, spread out in radiating directions, and become attached to its base. Besides the myoblasts already mentioned, the interior of the stalk is filled with mesenchymatous tissue, resembling that filling the space between the body-wall and the alimentary canal of the calyx.

(*c*). *The Neck*.—The extensive development of the ventral muscles and the continuity of many of the muscle fibers from stalk to calyx have produced an appearance at the junction of head and stem very unlike that commonly seen

in the Entoprocts. Generally, the neck is small and the infolding of the cuticle to form the septum is alike on all sides. The plug of cells usually occupies a central position, and the regenerative cells are of equal size and are symmetrically arranged. A very different condition prevails in *Myosoma*. The neck is stout and broad. On the ventral side the stalk extends part way up the calyx, as shown in polypides three and four of fig. 1. The plug of cells is nearer the dorsal than the ventral side, and the regenerative zone is not symmetrically disposed. Figure 3 represents these conditions in part. This section does not show the calyx in its natural or usual position. It is thrown backward too much and makes the plane of the lophophore almost horizontal. The evidence that this is an unnatural position is found in the distortion of the cells (fig. 3, *cl. cls.*) which bridge over the opening in the center of the septum. In the normal condition these cells should be horizontal. This very distortion gives the best view of the ventral muscle and it was for this reason that the section was chosen. If proper allowance be made, the thickness of the neck, the proximity of the plug of cells to the dorsal side, and the asymmetry of the regenerative zone are plainly manifest in fig. 3. Figure 13 represents the usual appearance of the neck in the Pedicellines. Comparison of this with fig. 1 will perhaps make the difference more obvious, although allowance must be made for a difference in magnification.

B. Regeneration.

Corresponding to this thickness of the neck, there is a firmness of attachment between stalk and calyx very different from the fragile connection usually presented by this family. In *Myosoma* the calyces do not drop off easily, at least in preserved specimens. Experimentation seems to show that there is a greater tendency to break away from the stolon than for calyx and stem to separate, especially in the case of the younger polypides. In attempting to separate polypide and stolon by pulling them apart, the stem, in each case, stretched considerably before any break

occurred. In older polypides, the separation took place just as often between stalk and stolon as between calyx and stalk. In younger individuals, out of fifteen experimented with, twelve broke either at the junction of stalk and stolon, or else part way up the stalk, and only three broke at the septum between stalk and calyx. Experimenting with other *Pedicellines*, the writer could in no case detect any stretching of the stalk. The calyx always separated at the septum and with the very slightest pressure. In the colonies of *Myosoma* which have been examined there is a remarkably small number of headless stems. It was only after a careful search among stems accidentally broken from stolons while tearing them out that a few were obtained upon which calyces were forming in various stages of development; so that, although *Myosoma* does not lose its calyces as easily as most Entoprocta, yet, if the loss occurs, regeneration does take place.

C. Discussion.

Myosoma spinosa is an extremely interesting form, both as an example of correlated and adaptive variation, and as a form which while exhibiting a high degree of specialization, yet shows marked affinities with more primitive Entoprocts, especially with *Loxosoma*.

The stem of all Entoprocts is characteristically muscular. The calyx, except for delicate sphincter muscles, is just as characteristically devoid of muscles. Two observers, Allman (1856) for *Pedicellina echinata*, and Van Beneden (1845) for *Pedicellina belgica*, speak of finding retractor muscles in the calyx of these species. Their results on this point have not been confirmed by other observers, but, even if correct, the muscles to which they refer have an entirely different function from the somatic ventral muscle of *Myosoma*. The function of a retractor muscle in the sense spoken of by these observers is to draw the tentacles within the sheath. Indeed, Allman speaks of a structure which he calls a sheath in *P. echinata*, into which the tentacles are retracted. The ventral muscle of *Myosoma*, however, does

not act as a retractor for the tentacles. It is closely connected with the longitudinal muscles of the stalk, both morphologically and functionally. The somatic portion together with the peduncular portion contracts the whole polypide upon the ventral side, forming the characteristic bow-shape so commonly assumed. The correlation of muscular development exhibited by *Myosoma* depends primarily upon the growth of the ventral muscle. Its action is antagonistic to that of the lophophoral sphincter; hence there follows the unusually strong development of the latter. In contraction, the ventral muscle draws the tentacular disc and the dorsal organs toward the ventral side. This would greatly diminish the space within the atrial cavity, which at certain seasons of the year, as when embryos are rapidly developing, would be a disadvantage. By the correlated growth of the atrial retractors the floor of the atrium is drawn downward and the space within is, in a measure, preserved.

Such muscles as are usually found in the calyx of the Pedicellinidæ, viz., the sphincter muscles, the tentacular muscles, and the body muscles mentioned by Ehlers for *Ascopodaria macropus*, are said to originate from the parenchymatous tissue of the calyx. It is difficult to conceive that such alone is the origin of the muscles of the calyx of *Myosoma*. In examining sections of the calyx, the assumption that the muscle fibers in the body arise in great part from those of the stalk, and that many of them have become secondarily divided, does not seem unreasonable. Such a hypothesis, however, can only be established by a study of the development of the polypide.

It is the open communication between the stalk and calyx of *Myosoma* which allies it so closely with *Loxosoma*. In the latter, the line of demarcation between body and stalk is not well defined. The muscle fibers of the stalk pass directly into the body, and, according to most observers, end somewhere in the lower part of the latter. In his account of *Loxosoma kefersteinii*, Nitsche (1869) says that the muscle fibers of the stalk are attached to the base of the stomach. Vogt (1876) in describing *L. phascolosomatium*

says that the muscle fibers are distributed over the base of the body. Other observers who say nothing of the distal attachment of the muscle fibers represent them in their drawings as extending a short distance into the calyx or body, and as radiating around the base of the stomach. Through the courtesy of Dr. W. S. Nickerson of the University of Minnesota, I have had the privilege of examining some specimens of his new species, *Loxosoma davenporti*, a complete report of which has not yet been published. I have prepared a few individuals *in toto*, staining and clearing them in oil, and the muscle fibers of the stem come out distinctly. The indications are that part, at least, attach themselves either to the floor of the atrium or to the body-wall in the vicinity of the atrium. The opacity of the organs of the body, however, prevents a clear view of the distal attachment of the muscles of the stem, although there is no doubt that they extend far into the body on the ventral side.

Seeliger (1889) gives an interesting stage in the development of *P. echinata* from the larva, wherein the elements of the stalk are directly continuous with those of the calyx; and he says, "Auf diesem Stadium ähnelt die junge *Pedicellina* einer *Loxosoma*, bei der ebenfalls die Sonderung in Stiel und Köpfchen nur unvollkommen ausgeprägt ist."

Our species shows other *Loxosoma* affinities. In his very interesting study of *L. phascolosomatum*, Vogt (1876) contrasts *Loxosoma* and *Pedicellina* in the following words: "Ce qui distingue, entre les points mentionnés par M. Nitsche, les *Pédicellines* et les *Loxosomes* en premier lieu, c'est la position de l'appareil tentaculaire et la conformation générale du corps. L'appareil tentaculaire est placé sur la face ventrale chez les *Loxosomes*, tandis qu'il se trouve au bout de l'axe de la tige et du corps chez les *Pédicellines*; le corps des *Pédicellines* est comprimé latéralement, celui des *Loxosomes* verticalement. * * * L'appareil tentaculaire est placé exactement au sommet chez les *Pédicellines*, sur le côté ventral un peu creusé chez les *Loxosomes*. Ce qui, chez les premières, se présente comme

un sac à ouverture centrale, montre chez les derniers la forme d'un capuchon serré sous le menton et tiré sur la tête. Si cette différence est sensible, je dois dire cependant que la tendance vers une formation semblable se montre déjà chez les Pédicellines, dont les deux faces, ventrale et dorsale, sont loin d'être symétriques. Comme chez les Loxosomes, la paroi du corps, le long de laquelle remonte le rectum et que nous avons nommée la face postérieure, est plus bombée que celle à laquelle est adossé l'œsophage. Un plan vertical et longitudinal, placé par la tige et le corps d'une Pédicelline qui montre son corps de la manière ordinaire, en présentant l'œsophage d'un côté et le rectum de l'autre, coupe bien en deux moitiés symétriques la couronne tentaculaire, mais non le calice. La moitié contenant le rectum est plus volumineuse, plus bombée que celle contenant l'œsophage. Ces rapports se laissent déjà voir dans les bourgeons, quoique à un degré moindre, et ne peuvent donc pas dépendre uniquement du développement de la poche incubatrice, située dans le voisinage du rectum. La conformation asymétrique est bien déjà dans le plan primitif des Pédicellines; mais elle y est seulement indiquée, tandis qu'elle est poussée à l'excès chez les Loxosomes, où elle va jusqu'au déplacement de la couronne tentaculaire."

The above might almost as well answer for a comparison of *Myosoma* and *Pedicellina*, for the former corresponds closely to *Loxosoma* in the displacement of the tentacular crown, the consequent obliquity of the lophophore, and the lateral compression of the body. The resemblance between *Loxosoma* and *Myosoma* is still further emphasized by the continuity of the muscle fibers of stalk and calyx, extending, if my observations upon *L. davenporti* be correct, even to the union of some of the muscle fibers with the floor of the atrium.¹

¹ Since writing the above, Dr. Nickerson has kindly furnished me with an outline of the musculature of *Loxosoma davenporti* previous to the publication of his paper on that animal. As far as can be learned from this, the arrangement of the muscles in *L. davenporti* and *M. spinosa* is strikingly similar. One especially interesting point is the existence of longitudinal muscle fibers which extend from the margin of the foot to the lophophore.

III. *Gonypodaria ramosa*, sp. nov.

PLATE XVI, FIGS. 13-16.

Diagnosis.—Zoarium composed of a chitinous branched segmented stolon, from each alternate segment of which stalks bearing polypides arise. Stalks merosarcine, furnished at their base and at intervals along their length with muscular dilatations from which branches proceed.

G. ramosa was first obtained at Pacific Grove by Professor H. P. Johnson of the University of California. It has since been found at Fort Point and Land's End, California, and on Channel Rocks, Puget Sound. A comparison of the colonies from these four localities leads one to suspect that there may be more than one species among them. They differ markedly in size and robustness of calyx and stalk, and especially in the number of branches. However, until more material can be obtained and further investigation made, they will all be placed under one species.

A colony of *Gonypodaria ramosa* presents an appearance very unlike the typical Entoproct. The stiff stems projecting to an unusual height and surmounted by their white calyces, the branching habit of growth and the stiff jerking movements, all contribute to make this Pedicellina an unique and interesting object of study. When examined closely the stalks are found to have the power of movement concentrated at definite points in barrel-shaped expansions, while the other portions are stiff and horny, and destitute of muscle fibers. Figure 13 represents part of a colony of *G. ramosa* and illustrates the characteristics mentioned above. The possession of several bulbous dilatations in the stalk places this form, at least provisionally, in the genus *Gonypodaria* Ehlers. The only other species of the genus known is *G. nodosa* Lomas (1886), described originally as *Pedicellina gracilis*, var. *nodosa*, and afterwards as *Ascopodaria nodosa*. These two species, *G. ramosa* and *G. nodosa*, differ in the number of muscular expansions on the stalk. The latter has not more than three, while *G. ramosa* has frequently four, five, or more. This in itself is not an

important difference, since in a colony of *G. ramosa* individuals resembling *G. nodosa* may be found. But the branching is peculiar to this form and warrants the formation of a new species.

A. Structure.

1. THE STOLON.—This is stout and thicker than the ascending stalks. It has a yellow color in the younger parts of the colony but becomes brown with age. It is covered by a thin, transparent cuticle continuous over stalk and calyx. Beneath the cuticle is a thick chitinous layer to which the color and rigidity of the stolon are due. It is divided at intervals by perforated septa into segments of varying length. A segment which does not bear a polypide is intercalated between two which do. Sometimes the polypide-bearing segments are crowded together, in which case the intercalated segments are very short, and the septa at their extremities are placed almost close together. The stolon produces branches at right angles to it, or nearly so. These grow from below the basal dilatation of an ascending stalk, and may appear on one side only, or opposite, on both sides. In no case has a branch been observed to grow from a non-polypide-bearing segment of the stolon.

2. THE STALK.—The stalk begins as a muscular dilatation resting upon the stolon. Above this it grows slender, but stiff and rigid. The occurrence of several of these dilatations divides the stalk into definite sections to which, following Ehlers, the name phalanx will be applied—a phalanx being considered to consist of a dilatation and the rigid portion arising therefrom (fig. 13, *pha.*). The distal phalanx, then, may frequently consist of a dilatation and a calyx, depending upon the stage of growth to which the stalk has attained. Since the musculature of the stalk is confined to these bulbous dilatations at the base of each phalanx, the stalk is of the type merosarcine. The basal or proximal dilatation arises from the stolon with a rather broad base, widening out somewhat into a barrel-shaped structure. It is covered by a thin cuticle which is distinctly

annulated, the annulations consisting of wrinkles or folds in the cuticle alone. Above the annulations the rigid portion of the phalanx begins, wide at the base, and narrowing somewhat suddenly into the slender, rigid portion. Each dilatation, then, is capped by a truncated chitinous cone. Beneath the thin cuticle of the dilatations the longitudinal muscle fibers are seen, forming an inner sheath or mantle. These are attached proximally to the stolon, and distally to the base of the cone which covers the top of the dilatation (fig. 13, *m. dil.*).

The rigid portion of each phalanx is covered externally by a thin cuticle continuous over stolon and basal expansion. Beneath is a thick chitinous layer, yellow or brown in color, resembling that of the stolon. In it, numerous pores occur irregularly disposed over the surface (fig. 13, *p.*). In longitudinal section these appear as deep, wide notches which are covered externally by the thin cuticle (fig. 16, *p.*). Similar pores occur in the stalk of *Ascopodaria macropus*, and Ehlers suggests that an opening to the outside may be found in them. There is no evidence for this in *G. ramosa*. The interior of the phalanx is filled with a mesenchymatous tissue continuous with that of the interior of the muscular dilatation. Near the base of the rigid portion of each phalanx a septum occurs. This is perforated and allows a free passage from one part of the stalk to another. The maximum number of phalanges in a stalk is six so far as the writer has observed. Four or five is a common number in the older parts of the colony. The description of the first phalanx, however, answers in the main, for all the others. As a stalk grows, the first calyx is differentiated before the rigid portion of the first phalanx has attained its full length. Before this time also, the first annulations of a second expansion appear below the calyx, so that by the time the calyx performs the function of nutrition it may have been carried into or above the second phalanx. Whether in this way the original calyx is carried to the summit of a stalk containing the maximum number of phalanges, or whether regeneration may occur before the maximum height is reached, is perhaps doubtful.

Branching.—From the distal portion of any phalanx branches may arise. Generally two opposite branches are produced, but frequently three may occur around the base of the same bulb. A branch is always separated from the parent stem by a double perforated septum (fig. 13, *dou. sep.*), so that, however twisted the growth may become, the branches may always be distinguished from the parent stalk. It is probable that branches begin to form at an early stage in the growth of the polypide. They are often found below the second dilatation, and frequently no difference can be discerned between the first phalanx of the branch and the second of the parent stalk except one of length. A branch may itself be composed of several phalanges similar in all respects to those of the parent, and the distal end of each of its phalanges may in turn give rise to secondary branches.

The complexity of growth is further increased in certain cases by the production of what may be called a stolon process in the place of a branch (fig. 16, *sto. pro.*). Such a process, like a branch, is separated from the parent stalk by a double perforated septum, and like a stolon, it forms alternate polypide-bearing and non-polypide-bearing segments (fig. 16, *non. pl. seg.*). Sometimes the segments are short, when dense masses of stems are formed about a single bulb as a center of growth (fig. 15). Sometimes a single long stolon is produced with segments of average length, thus forming a basis for a new growth of polypides. Transitions are often found between what has been called a simple branch and a stolon process. Thus, fig. 15 represents part of a parent stalk (*pa. stk.*) whose first lateral bud has produced a simple branch (*br. 1*). At the base of the latter another bud has produced a second branch (*br. 2*). A continuation of this process would produce a growth very closely resembling a stolon process, especially if that portion of the stem which is intercalated between the two septa (*in. seg.*) at the base of the two branches (*br. 1*, *br. 2*) should be somewhat prolonged. Such a case is represented by fig. 16. Here another stalk (*pa. stk.*) has produced a

branch (*br.*) and a stolon process (*sto. pro.*). This latter structure differs in no way from the true stolon attached to the substratum, except that it arises part way up the stem. It is composed of alternate polypide-bearing and non-polypide-bearing segments, and these vary in length just as they do in the original stolon. No hard and fast line, then, can be drawn between a polypide-producing branch and a stolon process; and that portion of the stem which is intercalated between the two septa at the base of an ordinary branch (fig. 15, *in. seg.*) may perhaps be homologous with the non-polypide-bearing segment of the stolon (fig. 13, *non. pl. seg.*) or of a stolon process (fig. 16, *non. pl. seg.*).

In the jointed character of the stalk and in the branching, *G. ramosa* bears considerable resemblance to *Arthropodaria benedeni* Foettinger (1887). In the latter, however, the differentiation of the muscular expansion has not been carried to the extent that appears in *Gonypodaria*. In the drawing given by Foettinger, the muscle fibers are represented to extend through the length of each segment or phalanx and the budding region appears to be about the middle of the expanded portion of the stem. In the character of their stems these two forms seem to be nearly allied to *Urnatella*. Davenport (1893) has discussed very fully the relationship between the segmentation of the stalk and the ability to produce buds. His remark upon the "suggestive parallelism" which exists "between the formation of segments and the production of buds" finds further confirmation in *G. ramosa*, where segmentation is complete and regular and is accompanied by the regular and constant formation of buds.

3. THE CALYX.—This differs in no essential respect from that described for the Pedicellinidæ in general. As a rule it is situated just above a muscular expansion. Its lophophore is at right angles to the axis of the stem. Externally it is covered by a continuation of the delicate cuticle of the stalk. The number of the tentacles varies from sixteen to nineteen. The various systems of organs, digestive, nervous, genital and excretory, correspond closely to those so fully described by Ehlers for *Ascopodaria macropus*.

B. Regeneration.

The union between stalk and calyx is extremely fragile, and as a consequence the calyces are frequently lost. A zone of regenerative cells occurs immediately below the calyx, as in other Pedicellines, and from this it is renewed. It is no uncommon thing to find a colony which has lost half of its calyces, while at the same time many regenerating ones occur. This species may be said to possess a second regenerative zone—that from which the branches arise. This region of branch formation is always in close relation with the bulbous dilatations. It lies just beneath them, and it is probable that it retains its power of external budding for only a short time—only until the thick layer of the cuticle becomes chitinized; but it seems to retain the power of regeneration from the inner layer of cells for a much longer time. An illustration of this is afforded by the condition represented in fig. 14. Here an old stalk (*o. stk.*) had lost calyx and upper phalanx, so that the distal end of the lower portion was left entirely exposed at a point just below where a muscular dilatation had occurred. At this part of the stem no septum is found. Yet from the inner layer of cells a young shoot has arisen with well differentiated calyx, basal dilatation, and rigid portion. In the discussion previously mentioned, Dr. Davenport maintains the importance of septa in enabling a regenerative zone to bud. On page 20, he says, "If we seek an explanation of the dissepiments, I think it is to be found in the protection of the stock against the influx of water and destroying organisms at the time of the loss of calyx or lateral branches which would make regeneration impossible." At the same time this writer holds (p. 21) that "segmentation has succeeded, rather than preceded, the condition of bud formation from the stalk, it being desirable owing to the greater danger from mutilation to which the stalk is exposed." From this point of view, *G. ramosa* retains a primitive capacity in a high degree in its ability to regenerate from a point where no septum has developed.

C. Movement.

A living colony of *Gonypodaria* presents a scene of considerable activity. Movement is greatest in the upper dilatations of the stalk, especially in the one at the base of distal rigid portion. Two movements can be detected, one from side to side, which is stiff and jerky, the other, a circular movement. In the first, the phalanx bends almost at right angles to one side, then to the other, and in the return to its original upright position it executes a partially circular movement. It is not possible to say whether or not the polypides respond to stimulus. Upon touching one with the dissecting needle there seemed sometimes to be response, but one could not be sure but that the movement might have taken place without such stimulus. There was no united, wave-like movement throughout the colony, such as Ehlers describes for *A. macropus*. What the stimulus is, it is difficult to say, especially when, as Ehlers also found in *A. macropus*, one sees stems which have lost their calyces execute the same movements as those which possess them.

IV. SUMMARY.

1. The new genus *Myosoma* is distinguished by the possession of a somatic ventral muscle which is continuous with that of the stalk and forms the great ventral muscle.

2. The somatic portion of the ventral muscle sends branches to each side of the œsophagus. These form the atrial retractors. It is probable that part of these branching fibers are connected with the genital ducts.

3. The musculature of the stalk consists of the longitudinal muscle fibers of the ventral muscle, and also of oblique fibers which proceed from the dorsal to the ventral side.

4. The tentacles contain each a pair of muscles, and the sphincter of the lophophore attains an unusual development.

5. Owing to the continuity of the ventral muscle, the neck of *Myosoma* is unusually broad and holds the calyx more securely upon the stalk than is the case in other *Pedicechinidæ*.

6. This communication between stalk and calyx, and the continuity of muscle fibers from one part of the polypide to the other, together with the oblique setting of the lophophore, allies *Myosoma* rather closely with *Loxosoma*.

7. The new species, *Gonypodaria ramosa*, is distinguished by the possession of a branching stalk. The branches arise from any bulbous dilatation, and are of two kinds, simple and stoloniac.

8. It is difficult to draw a real distinction between these two kinds of branches. Transitions between them can often be found.

9. A septum is found below the calyx and above each muscular dilatation of the stalk. A double septum is produced at the origin of a branch.

10. That part of the branch which is enclosed by the double septum may perhaps be homologous with a non-polypide-bearing segment of the stolon.

11. Regeneration of a stalk from the inner layer of cells at the base of a muscular dilatation may take place, even though the whole upper portion of the stem with the muscular dilatation be broken away.

V. IDENTIFICATION OF KNOWN SPECIES.

The following is a list of the species of Entoprocta found on the Pacific Coast, which have been previously described. The classification given by Ehlers has been followed.

Pedicellina Sars.

Pedicellina echinata Sars.

Pedicellina echinata Sars, Beskrivelser og Jagttagelser, 1835.

Pedicellina cernua (PALLAS) HINCKS, Brit. Mar. Polyzoa, Vol. I, p. 565.

Habitat.—Lime Point, California. Found growing on old hydroid stems together with *Eucratea chelata*.

Ascopodaria Busk.**Ascopodaria gracilis Sars.**

Pedicellina gracilis Sars, Beskrivelser og Jagttagelser, 1855, p. 6.

Pedicellina gracilis HINCKS, Brit. Mar. Polyzoa, Vol. I, p. 570.

Habitat.—Lime Point and San Pedro, California.

Ascopodaria macropus Ehlers.

Habitat.—San Pedro, California. Small quantities of this species have been obtained at various times from San Pedro, where it seems to be fairly abundant.

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January 2, 1900.

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ABBREVIATIONS USED IN THE FIGURES.

ap. sep.—aperture of septum.
at. re.—atrial retractor.
at. fl.—atrial floor.
atr.—atrium.
bas. r.—basal rib.
br.—branch.
br. so. v. m.—branch of somatic ventral muscle.
cls. l.—"liver cells."
cl. cls.—closing cells of septum.
cls. at. fl.—cells of atrial floor.
cls. g. d.—cells of genital duct.
cu.—cuticle.
chi. l.—chitinous layer.
dor. s.—dorsal side.
dor. m.—dorsal muscle.
dor. sep.—dorsal septum.
dor. w.—dorsal body-wall.
ec. stk.—ectoderm of stalk.
ec. ca.—ectoderm of calyx.
ec.—ectoderm.
gn.—ganglion.
int.—intestine.
in. seg.—intercalated segment.
loph. f.—lophophoral fold.
m. dil.—muscular dilatation.
m. g. d.—muscles of genital duct.
m. stk.—muscle of stalk.

non. pl. seg.—non-polypide-bearing segment.
nu.—nuclei.
æs.—æesophagus.
o. m. f.—oblique muscle fibers.
o. stk.—old stalk.
pa. stk.—parent stalk.
p.—pore.
pha.—phalanx.
re. cls.—regenerating cells.
rec.—rectum.
sag. r.—sagittal rib.
spl. reg.—spineless region.
sto.—stolon.
so. v. m.—somatic ventral muscle.
sep.—septum.
sph. loph.—sphincter of lophophore.
st.—stomach.
stk.—stalk.
sto. pro.—stolonic process.
suc. pl. seg.—successive polypide bearing segments.
sum.—summit of calyx.
tent. m.—tentacular muscles.
ten. r.—tentacular rib.
v. s.—ventral side.
v. m.—ventral muscle.
v. m. stk.—ventral muscle of stalk.
v. w.—ventral body wall.

EXPLANATION OF PLATE XVI.

All drawings made with the aid of a camera lucida, except figs. 1 and 13.

- Fig. 1. Part of a colony of *Myosoma spinosa*, gen. nov. The two stolons which are represented were not actually growing side by side, but were chosen to show the variability in segmentation. They are, however, typical. The arrangement of the younger polypides is somewhat diagrammatic, but each individual is as faithful a copy as could be made. $\times 25$.
- Fig. 2. A single polypide of *Myosoma spinosa*, showing a characteristic position, and the arrangement of the muscle fibers in the stalk. $\times 75$.
- Fig. 3. Para-sagittal section of the same through calyx and part of stalk, to show the somatic ventral muscle and its continuity into the stalk. $\times 300$.
- Fig. 4. Frontal section of the same, close to ventral wall of stomach. It shows the continuity of the muscle fibers from stalk to calyx, and also a few fibers of the branches of the ventral muscle. $\times 300$.
- Fig. 5. Cross-section of the calyx showing the branches of the somatic ventral muscle which form the atrial retractors. Section near the base of the oesophagus. $\times 130$.
- Fig. 6. Same as above (fig. 5), but three sections higher. $\times 130$.
- Fig. 7. Same as the two preceding figures, the section passing through the point where the atrial floor (*cls. at. fl.*) begins to appear. $\times 130$.
- Fig. 8. Sagittal section of calyx of *M. spinosa*, showing the connection of muscle fibers with the genital duct. $\times 650$.
- Fig. 9. Cross-section near the base of three tentacles of the same, to show the tentacular muscles. $\times 300$.
- Fig. 10. Longitudinal section of the same. $\times 300$.
- Fig. 11. Cross-section of the stalk of *M. spinosa* a few sections below the calyx, showing greater thickness of the muscle sheath on the ventral side. $\times 130$.
- Fig. 12. Same as the preceding, except that the section passes through the lower part of the stalk. $\times 130$.
- Fig. 13. Part of a colony of *Gonypodaria ramosa*, sp. nov. $\times 15$.
- Fig. 14. Part of an old stalk of *G. ramosa*, the distal end of which shows a regenerating polypide. $\times 100$.
- Fig. 15. A cluster of branches formed at the base of a muscular dilatation of the parent stalk. A transition from simple branching such as is shown in fig. 13, and stolon branching is indicated by the growth of a second branch (*br. 2*) from the basal dilatation of the first (*br. 1*). $\times 100$.
- Fig. 16. Represents a simple branch and a stolon process growing from the base of a muscular dilatation of the parent stalk. $\times 100$.